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OBSERVATIONS ON THE BIOLOGY AND LIFE HISTORY OF THE NET-WINGED MIDGE *DIOPTOPSIS SEQUOIARUM* (ALEXANDER) (DIPTERA: BLEPHARICERIDAE)

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The species *sequoiarum* Alexander was originally described in the genus *Philorus* Kellogg and subsequently moved to *Dioptopsis* by Alexander (1958). *Dioptopsis* includes species from Japan, Kashmir, southeast Europe, central Asia, and western North America (Alexander, 1958). *Dioptopsis sequoiarum* is one of five species that occur in the western United States (Hogue, 1970, 1973).[1]

Few biological and behavioral data are available on blepharicerids occurring in the United States. Observations have been made on an eastern species, *Blepharicera capitata* Loew (Kellogg, 1900) (cited by Gibo, 1964 as *B. tenuipes* Walker). Also available are short notes on several species (Kellogg, 1903), an account of collection habitats for *Dioptopsis dismalea* Hogue (Hogue, 1970), and extensive studies on *Blepharicera micheneri* Alexander and *Philorus yosemite* (Osten Sacken) in California (Gibo, 1964).

In the present paper we provide new observations and data on the biology and behavior of a little-known species, *Dioptopsis sequoiarum.* An attempt is made to correlate morphological features, illustrated with scanning electron micrographs, and hydrophobic properties of the teneral adult cuticle. We will relate sex ratios in various life stages and habitats to sexually dimorphic behavior patterns. Salient features of the biology of *D. sequoiarum* are compared with those of the better known California genera.

Methods and Materials

Study site.—Our study was conducted along an 11.5 km section of Sagehen Creek, Nevada County, California. Beginning at the intersection of Sagehen Creek and Rt. 89, the section extended west and parallel with Sagehen Creek Road.

The area we studied most extensively was 10 km west of the Rt. 89 junction, a point where Sagehen Creek passes under Sagehen Road through a large culvert. We designated this area the culvert study site. It includes a rectangular area 10 m either side of the creek, 25 m either side of the culvert. The creek flows from the northwest through the culvert and then bends to the east. The study site is bounded at either end by stands of aspen, lodgepole pine, and fir. Above and below these boundaries the creek is narrow, deep and winding with numerous waterfalls and logjams. The canopy is dense, and most of the creek is in deep shade.

Within the culvert study site the creek is straight, wide (4.5 m) and uniformly shallow (2–10 cm). The creekbed passes down a uniform 7% grade and is composed of fine gravel densely overlaid with rocks ranging in size from 4–80 cm. Vegetation along the margin of the culvert study site was largely cleared away during construction of the culvert, so, with the exception of a few clumps of willow, the creek is open to the sky.

The rest of Sagehen Creek is typical of high, cold eastern Sierra streams passing through meadows or over beaver dams. The elevation varies from 7000′ at the western end of the study area to 5200′ at the intersection of the creek and Rt. 89.

Methods.—Standardized sweepnet surveys (Bowen et al., 1980) were conducted at various distances away from the creek at several localities including the culvert study site. Undisturbed adults were also counted in the culvert and other resting sites. In both of these surveys, sex ratio data were also collected. Emergence behavior was observed by removing rocks with pupae to more calm margins of the creek. These rocks were positioned so that the pupae were constantly washed with a few millimeters of water.

Various substrates were characterized and surveyed for pupae and larvae. Samples of all life stages were collected and preserved in 4% isotonic (pH 7.4) glutaraldehyde or 70% ethanol. The glutaraldehyde specimens were then dehydrated and critical-point dried for examination with a scanning electron microscope.

Results

All life stages, except eggs, were found in a few high density patches along or in the 11.5 km portion of Sagehen Creek. During both seasons, the densest population discovered was at the culvert study site. *D. sequoiarum* did not occur below 6000′, although occasional adult females were taken at a lower elevation.

Larvae.—The larvae were found exclusively on submerged, smooth rock substrates. Exposed roots, submerged logs, organic debris, spray-moistened rocks and the like, though available, were not used. Larvae were found most commonly in shallow, 1–4 cm, fast-moving white water, on the top, lateral and downstream aspects of rocks. They could also be found at greater depths but only at the base of small waterfalls or where water passed over the top of large rocks creating a deep, turbulent white water basin. In these circumstances, larvae were found as deep as 15 cm. The specific locality in the stream seemed to be independent of the distance from the shore, but seemed to be correlated with areas of higher light intensities.

Two forms of larval locomotion were observed. The first, a slow, forward progression was achieved by successively detaching, advancing, and reat-

Table 1. Sex ratio data from surveys conducted at Sagehen Creek.

Date	Study site	Distance from creek	Life stage	Female	Male	Ratio
23 July 1980	Culvert	—	Pharate adult	27	10	2.7:1.0
		—	Adult	2	19	1.0:9.5
1978, 1980*	All	Less than 10 m	Adult	12	166	1.0:8.4
		Greater than 10 m	Adult	9	2	4.5:1.0

* The 1978, 1980 data are summed over the entire study period, at all sites along the 11.5 km Sagehen Creek section.

taching each ventral sucker individually. Dorsally, this appeared similar to rhythmic caterpillar motion and constituted normal locomotion. The second, a quick, lateral movement was observed only after the application of intense stimuli. The anterior or posterior suckers were rapidly detached, and the free end of the larva was adducted laterally so that the larva assumed a slight crescent shape. The free suckers were then reattached and, on the opposite end, were detached. Three or four complete replications of this sequence, the average number observed in a single event, displaced the larvae roughly 1 cm from the point of stimulation. This is apparently an evasive response.

The larval density on individual rocks was fairly low, 1 per 4 cm^2. This distribution seemed highly consistent and regular as if each larva was exerting some form of territoriality.

Pupae.—Pupae were restricted to the same microhabitats and substrates as the larvae. However, pupae were nearly always found in very dense clusters of 3–180, rarely deeper than 3 cm.

Pupal orientation was governed by the direction of current flow. The median, longitudinal axis of the pupal case was parallel to the microcurrent, with the head oriented downstream. Because the turbulence around the irregularly shaped and placed rocks was so complex, the orientation of any two pupae in the same cluster was usually somewhat different, although in some clusters, even subtle orientation differences were indistinguishable.

Of 54 pupae collected on 23 June 1980 (see Table 1) at the culvert site, 40 were females and 14 were males, a ratio of 2.9:1.0.

Eclosion.—On several occasions teneral adults were observed emerging directly from torrential water, short distances downstream from pupal clusters. The following account is a synopsis of the behavior of three eclosing adult female flies observed on 13 and 22 July 1980 at the culvert study site. The pupae were on rocks which were moved to slow, clear water at the creek margin.

The pupal skin split down a median, dorsolongitudinal line through which the head emerged first. Slowly, over the next 5 min, the thorax appeared, and the halteres were erected. In the next 3 min, the wings longitudinally unfolded and began flapping. The wings were very soft and grey and did not unfold to full width until after flapping had commenced. Next, the very narrow abdomen was pulled from the pupal skin, followed by the legs. The insects remained attached to the pupa for 1–2 min, and then detached. They were carried downstream a short distance and, reaching the surface, immediately took flight. The wings never ceased beating during the entire process. The teneral adult, including wings, was completely grey, except for the eyes. The upper half of the eye was red and the lower was black. The whole insect was very soft and easily damaged. Eclosion, under these unnatural circumstances, required 8 min.

During the entire eclosion process, both under water and once they reached the surface, the insects remained completely dry. When submerged, the entire fly was covered with a silvery sheen presumably due to a thin film of air. When attempts were made to wet freshly killed specimens with glutaraldehyde fixative, an acutely negative meniscus formed at points of contact. Subsequent ultrastructural investigations revealed the entire cuticular surface of the adult to be covered with a dense mat of microtrichia (Figs. 1–7). This mat varied in structure and density on different areas of the body and was present even on the wings, eyes, and halteres.

Adults.—Adults were found in groups most commonly underneath logs overhanging the creek in shady situations. Large numbers were observed on the ceiling of the culvert. Individuals were also collected with sweepnets at various distances from the stream (Table 1).

Adult *D. sequoiarum* were normally abundant on the culvert ceiling at midday and rare or absent after 1800 hr. On four nonconsecutive days, adults were counted between 1100 and 1400 hr and again between 1800 and 1900 hr. The mean frequency at midday was 14 whereas, in the evening, it had dropped to 0.25.

Discussion

Dioptopsis sequoiarum closely resembles *D. dismalea* in general habitat choice (Hogue, 1970). Common characteristics include occurrence in open sections of stream, proximity to meadows, aspens, small willow thickets,

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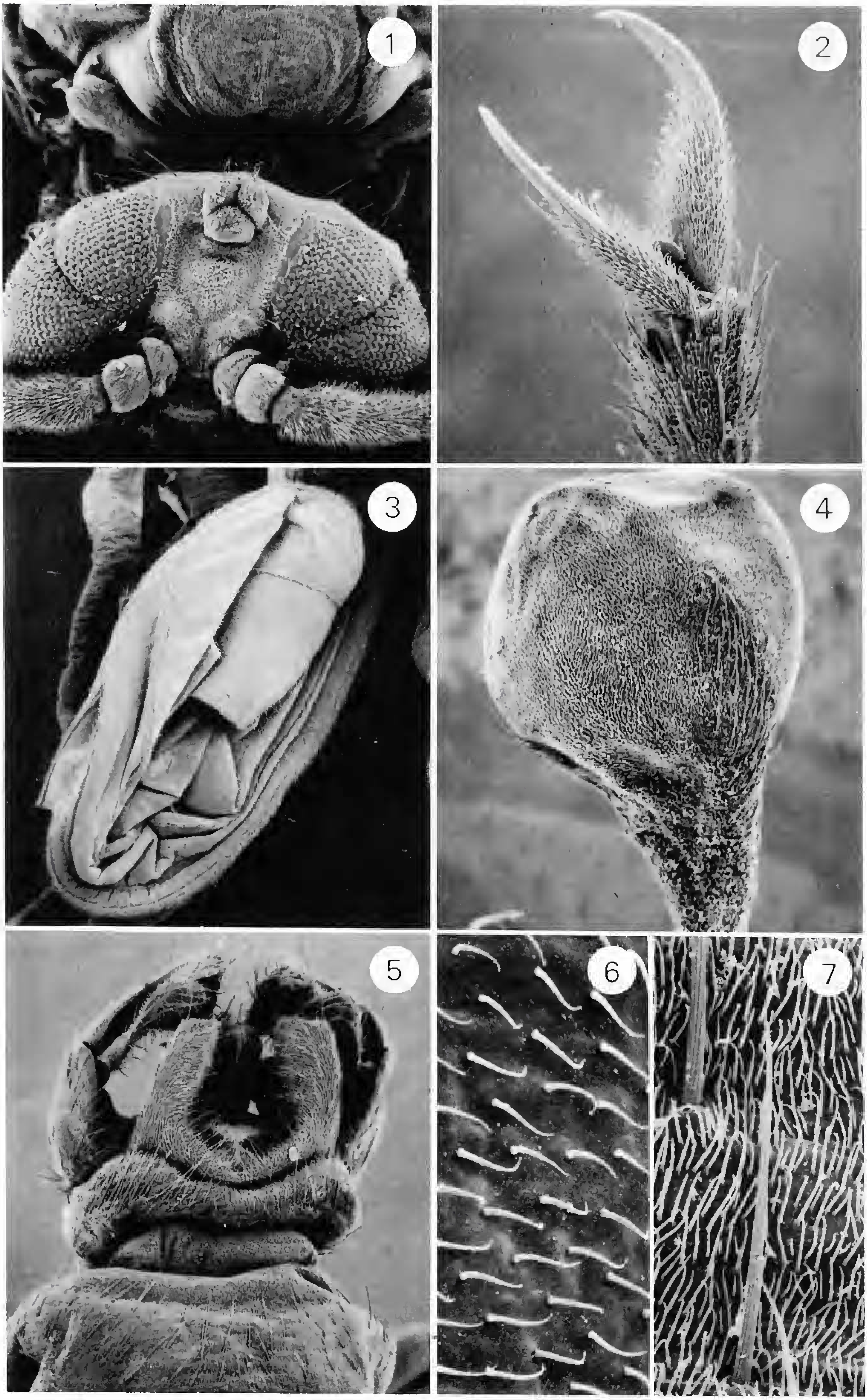
Figs. 1–7. Fig. 1. Head and mesoscutum of pharate male, ×8. Fig. 2. Tarsal claw of teneral female, ×300. Fig. 3. Wing dissected from pharate adult female, ×40. Fig. 4. Haltere of teneral female, ×148. Fig. 5. Terminalia of pharate male, ×79. Fig. 6. Magnification of wing microtrichia, in Fig. 3, ×700. Fig. 7. Magnification of dorsal microtrichia on abdomen in Fig. 5, ×800.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and for the most part, the most torrential water. Descriptions of larval and pupal habitat correspond almost exactly.

Of the two species, *Blepharicera micheneri* and *Philorus yosemite,* studied by Gibo (1964), *B. micheneri* was closest to *D. sequoiarum.* The larvae of *B. micheneri* were found on submerged rocks or rocks at the base of waterfalls, at a depth (5.08 cm) comparable to that of *D. sequoiarum* (1–4 cm). The distribution of larvae was similar; 1 cm apart in *B. micheneri* and 1 per 4.0 cm^2 for *D. sequoiarum.* Pupal orientation was somewhat similar; Gibo described pupae of *B. micheneri* aligned with the current in fast-moving water, but not strictly so in the slow parts of the stream. All pupae we found were in fast-flowing streams, where they were aligned with the current. The distance from the surface at which pupation occurred was very similar; 1.27 cm for *B. micheneri* and not deeper than 3.0 cm for *D. sequoiarum.*

Aggregations of adult *Dioptopsis sequoiarum* were found in resting sites similar to those occupied by *Blepharicera micheneri.* These sites were characterized by moist cool shade and close proximity to the stream. *D. sequoiarum* were never found in aggregations at distances greater than a few meters from the stream or in direct sunlight, as were *Philorus yosemite. D. sequoiarum* prefer to hang upside down from surfaces overhead, rather than on vertical or horizontal surfaces. These aggregations were composed principally of males.

The sex ratio data, reported above for the various times and localities, provided some insight into the various aspects of adult behavior. On 23 July, the ratio of soon-to-emerge pupae were skewed to females, 2.7:1.0, whereas, in the culvert resting site, males were the most common, at 1.0:9.5. The latter figure is closely correlated with the ratio observed 10 m or less from the stream, during the entire study. However, the ratio reverses in favor of females at distances greater than 10 m from the creek. We hypothesize this shift in ratios is probably caused by a dimorphism between male mating behavior and female oviposition site selection. Males may tend to stay near the stream where the likelihood of mating with newly-emerged, virgin females is fairly good. Females, on the other hand, could be the invasive, colonizing form, flying considerable distances after copulation, in search of new oviposition sites. Variation in this behavior could account for the few females that stay close to the eclosion site assuring the population for the following year, and for the occasional stray male found great distances from the stream. This hypothesis was supported by the observation of two females apparently ovipositing in very small rivulets, completely unsuitable for larval development, 3.2 km from any known larval habitat. Males may also emerge earlier in the season than females, similar to what one observes in a generation of mosquitoes. This phenology might explain the dominance of mature female pupae on 23 July, late in the season.

There are at least two specializations of teneral midges that adapt them to torrential habitats. The first is the wing-folding pattern; visible as the net-like pattern between veins after which the group is named. The wings are developed to full length and width in the pupae and at eclosion are immediately available for flight. Actually, they are already beating before emergence from the pupae is complete. The second adaptation is the mat of hydrophobic microtrichia which, on *D. sequoiarum,* cover the entire body. These structures probably retain the plastron, keeping the insect dry, and break the surface tension as the midge takes flight from the torrential stream. Additionally, the soft, unsclerotized cuticle common to all teneral insects may be especially important to blephariceridss, preventing permanent damage by the action of white water during eclosion and before taking flight. In support of this idea, teneral insects collected as they emerged had legs bent and curled almost everywhere but at the real joints. Teneral flight is commonly observed in other Nematocera, as well as Ephemeroptera, and Odonata. But, blephariceridss seem to have developed this habit to an extreme.

It is interesting to note that the unique qualities of the culvert study site (i.e., its straightness, overhanging ceiling, width and shallow depth) are completely artificial. Most of these attributes were created when the bridge and culvert were constructed in the early 1960's. The culvert study site has, by far, the most dense population of *D. sequoiarum,* an example of environmental perturbation by man that may have increased the frequency of an otherwise rare insect.

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Footnote

[1] "Blepharicerid taxonomists advise that this and other North American species in the genus '*Dioptopsis*' are not congeneric with the type from southeast Europe. The generic placement used here is provisional only until the relationships of the species are known." (C. L. Hogue, pers. comm.)